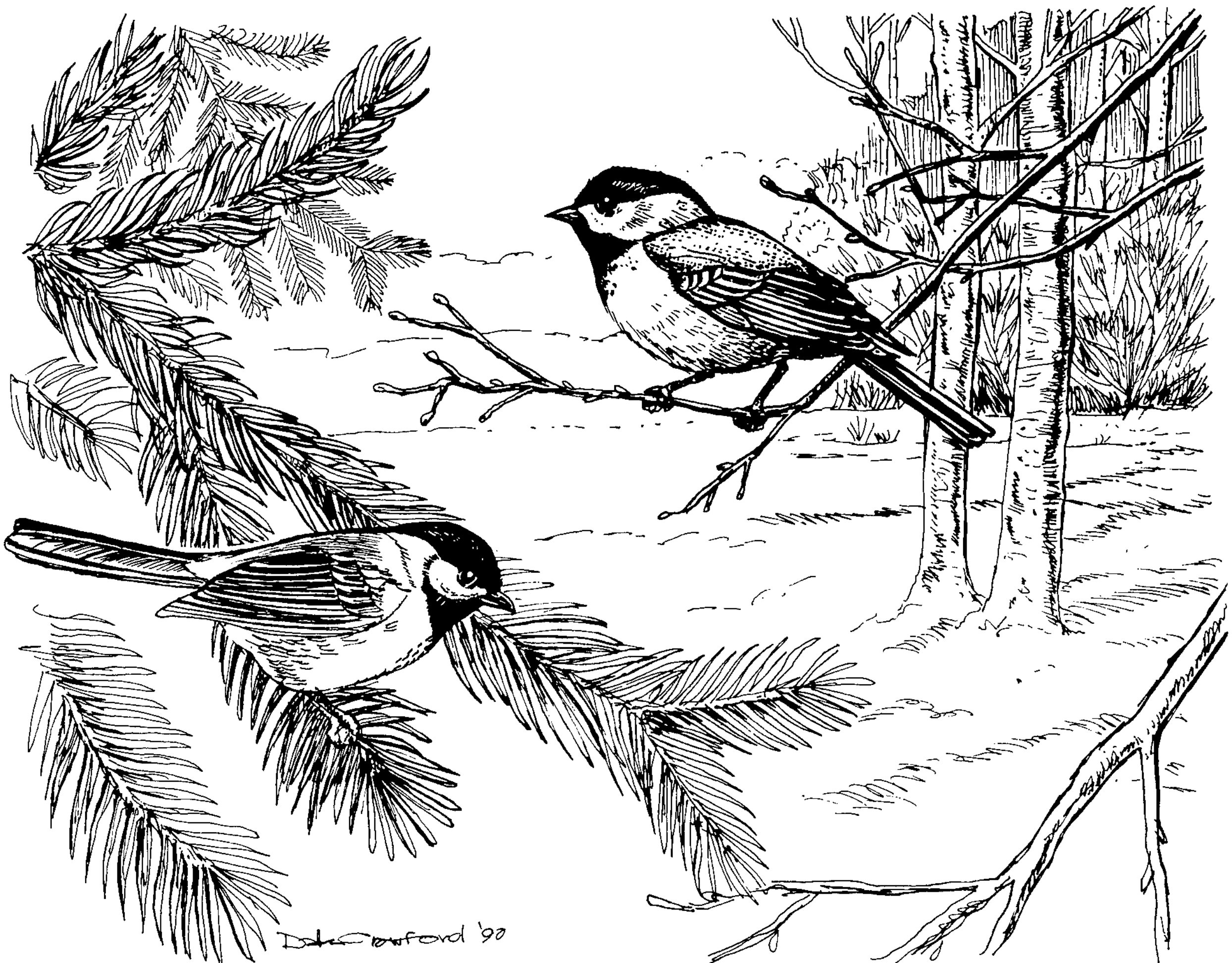
Biological Report 90(10)
October 1990

Tests of a Habitat Suitability Model for Black-capped Chickadees



Fish and Wildlife Service
U.S. Department of the Interior

Biological Report

This publication series of the Fish and Wildlife Service comprises reports on the results of research, developments in technology, and ecological surveys and inventories of effects of land-use changes on fishery and wildlife resources. They may include proceedings of workshops, technical conferences, or symposia; and interpretive bibliographies.

Copies of this publication may be obtained from the Publications Unit, U.S. Fish and Wildlife Service, 1849 C Street, N.W., Mail Stop 130–ARLSQ, Washington, DC 20240, or may be purchased from the National Technical Information Service (NTIS), 5285 Port Royal Road, Springfield, VA 22161.

ISSN 0895-1926

Biological Report 90(10)
October 1990

Tests of a Habitat Suitability Model for Black-capped Chickadees

By

Richard L. Schroeder

U.S. Department of the Interior
Fish and Wildlife Service
Washington, D.C. 20240

Contents

Tests of a Habitat Suitability Model For Black-capped Chickadees

by

Richard L. Schroeder

U.S. Fish and Wildlife Service
National Ecology Research Center
4512 McMurray Avenue
Fort Collins, Colorado 80525

ABSTRACT.—The black-capped chickadee (*Parus atricapillus*) Habitat Suitability Index (HSI) model provides a quantitative rating of the capability of a habitat to support breeding, based on measures related to food and nest site availability. The model assumption that tree canopy volume can be predicted from measures of tree height and canopy closure was tested using data from foliage volume studies conducted in the riparian cottonwood habitat along the South Platte River in Colorado. Least absolute deviations (LAD) regression showed that canopy cover and overstory tree height yielded volume predictions significantly lower than volume estimated by more direct methods. Revisions to these model relations resulted in improved predictions of foliage volume. The relation between the HSI and estimates of black-capped chickadee population densities was examined using LAD regression for both the original model and the model with the foliage volume revisions. Residuals from these models were compared to residuals from both a zero slope model and an ideal model. The fit model for the original HSI differed significantly from the ideal model, whereas the fit model for the revised HSI did not differ significantly from the ideal model. However, both the fit model for the original HSI and the fit model for the revised HSI did not differ significantly from a model with a zero slope. Although further testing of the revised model is needed, its use is recommended for more realistic estimates of tree canopy volume and habitat suitability.

The U.S. Fish and Wildlife Service (Service) has published Habitat Suitability Index (HSI) models (Schamberger et al. 1982) for more than 150 species of fish and wildlife. These models were developed primarily from literature sources and expert reviews and provide a quantitative method to predict habitat suitability based on vegetative and physical characteristics of habitats. Whereas earlier Service efforts were directed at model development, the emphasis in recent years has shifted to tests of published model hypotheses (Schamberger and O'Neil 1986). I present results from tests of hypotheses in the black-capped chickadee (*Parus atricapillus*) HSI model (Schroeder 1983), as well as an empirical test of the HSI model itself.

The black-capped chickadee HSI model provides a quantitative rating of the capability of a habitat to support breeding, based on measures related to food and nest site availability (Fig. 1; Table 1). The food portion of the habitat model was developed from data presented in Sturman (1968) and assumes that black-capped chickadee population densities are related to arthropod abundance and that this is positively correlated with tree foliage volume. Sturman (1968) found that canopy volume of trees was a strong predictor of black-capped chickadee abundance ($r^2 = 0.796$). However, measures of tree canopy volume as presented in Sturman (1968) are very time consuming and may not be suitable for many users of the HSI model. An alternative method is presented in the HSI model, based on the assumption that measures of tree heiGht and tree canopy closure can be used in place of Sturman's volume measurements to assess the suitability of the food resource for black-capped chickadees.

The nest site availability portion of the HSI model assumes that reproduction, and hence black-capped chickadee numbers, may be limited by the density of snags that are 10 to 25 cm diameter at breast height (dbh). This part of the model incorporates estimates of the number of suitable snags per unit area that are assumed to be required by breeding black-capped chickadees.

The black-capped chickadee HSI model was also tested in New York by Bayer and Porter (1988). They compared population densities and HSI model values for 28 sites using both continuous and discrete (>0.5, >0–0.5, and 0) HSI values. The model was successful in predicting population abundance at the discrete level ($P < 0.05$) but not at the continuous level.

The objectives of this study were (1) to test the hypothesis that tree canopy volume can be predicted from meas-

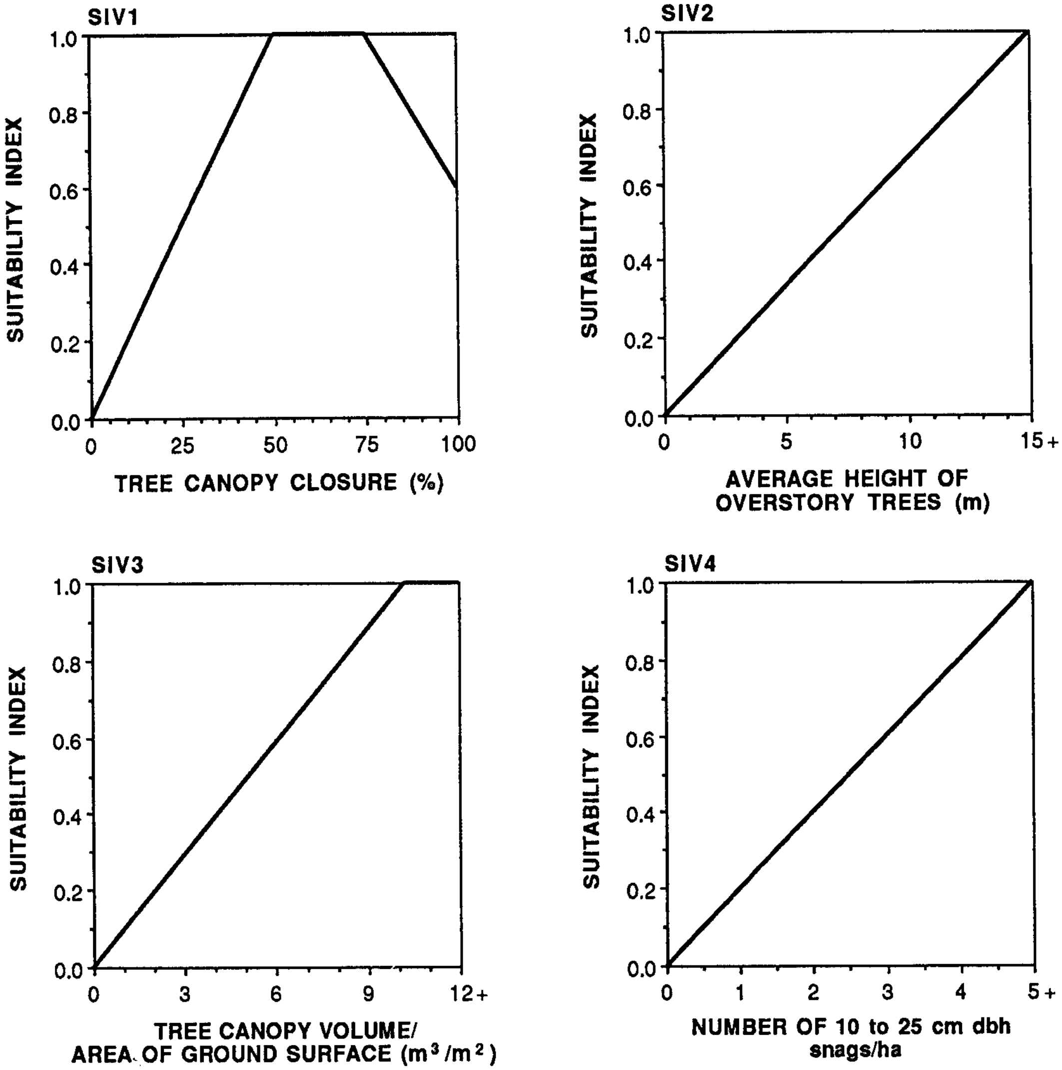


Fig. 1. Habitat variable and suitability index graphs for the original black-capped chickadee HSI model (Schroeder 1983).

ures of tree height and canopy closure, and (2) to test the relation between the HSI and estimates of black-capped chickadee densities during the breeding season.

Study Area and Methods

Foliage volume studies were conducted in plains cottonwood (*Populus sargentii*) bottomland along the South Platte River near Crook, Logan County, Colorado. Black-capped chickadee population data were obtained from previous studies in the same area conducted by Sedgwick and Knopf (1986; J. A. Sedgwick and F. L. Knopf, U.S. Fish and Wildlife Service, Fort Collins, Colorado, unpublished data). Elevations along the South Platte River ranged from 1,116 to 1,149 m, and plains cottonwood was the dominant overstory tree species. For further descriptions of the riparian vegetative community refer to Sedgwick and Knopf (1986).

Volume Test

A major assumption in the HSI model is that the food suitability index (SI) computed through measuring tree height and canopy closure is equivalent to the food SI

Table 1. *Life requisite and HSI determination methods for the black-capped chickadee (*Parus atricapillus*) HSI model (Schroeder 1983).*

Model output	Determination method
Food suitability index (SI)	$(SIV1 \times SIV2)^{1/2}$ *or* (SIV3)
Nest SI	SIV4
HSI	Lower of food SI or nest SI

value computed for tree canopy volume as measured using Sturman's (1968) methods. If this assumption of equivalence is true, canopy volume can be predicted from tree height and canopy closure by calculating the food SI for tree height and canopy closure and then determining the canopy volume associated with the food SI from the graph of SIV3 (tree canopy volume). A food SI of 1.0 produced through measuring tree height and canopy closure should indicate a tree canopy volume $\geq 10.2\ m^3/m^2$ of ground surface. The null hypothesis for the tree canopy volume test is that for tree canopy volumes $<10.2\ m^3/m^2$ ground surface there is a linear ratio of 10.2:1 between tree canopy volume predicted using the methods of Sturman (1968) and the food SI determined through the use of tree height and tree canopy closure, with an intercept of 0.

To test this hypothesis, detailed measurements were taken of each tree (minimum height of 5 m) on plots selected to provide wide variation in the amount of foliage volume estimated to be present. Eighteen plots were selected with plot sizes of 0.04 ha except for 3 0.1-ha plots in scattered mature cottonwood stands and 2 0.01-ha plots in dense cottonwood sapling stands.

Measurements to determine the volume of living foliage of each tree were taken in May 1988, following the methods described in Sturman (1968). Tree height measurements were taken with a clinometer at a measured distance from each tree. The width of individual tree canopies was measured by vertically projecting the inner and outer portion of the living foliage and marking these points on the ground with wire flags.

The percent of tree canopy cover within each plot was measured with a spherical densitometer (Lemmon 1956) at 20 points, equally spaced along 2 diagonal transects. The densitometer was modified to reduce the overhead angle viewed in the mirror by using only the four center squares. This technique ensured that canopy cover readings were nearly vertical and did not take in vegetation outside the plot. A hit or miss was recorded on each of four points within each mirror square.

Measurements of tree dbh were taken to determine basal area for each plot. Basal area measurements were not required in the original HSI model. However, basal area is widely used and was measured to determine the relation between it and tree canopy volume.

HSI Model Test

The null hypothesis for the test of the HSI model is that regression of the HSI on estimated black-capped chickadee population densities will produce a model with a slope significantly different from zero but not significantly different from the slope of a model predicting maximum expected population densities. Black-capped chickadee breeding population data from previous studies (Sedgwick and Knopf 1986 and unpublished data) were used to test this hypothesis. These data were collected on 10 16-ha plots in riparian cottonwood stands in 1982 and 1984–86, using the variable circular-plot method (Reynolds et al. 1980). Black-capped chickadee population density estimates were determined by using program TRANSECT (Burnham et al. 1980). Tree heights were measured with a clinometer. Data on snag density, as defined in the HSI model, were not collected; however, the number of trees with cavities (any opening 3 to 12 cm in diameter) was recorded. Based on the scarcity of snags on the study site (0.66 snags per hectare), and the fact that most cavities (95.8%) were in live trees, it seems that the number of trees with cavities provides a reasonable substitute for the snag density data required in the HSI model. Additional descriptions of methods for population estimation and vegetation measurement are presented in Sedgwick and Knopf (1986). I obtained measurements of tree canopy closure from low-level aerial photographs of each of the 10 plots. Individual canopies of cottonwood trees were outlined on an acetate overlay of the photographs, and digitized. Tree canopy cover was computed by comparing the total area of the tree canopies to the area of each plot.

Statistical Analyses

I used least absolute deviations (LAD) regression (Barrodale and Roberts 1974) to examine linear relation between (1) tree canopy volume predicted from tree height and canopy closure, and canopy volume estimated following Sturman (1968), and (2) black-capped chickadee densities and HSI values. Least absolute deviation regression is more resistant to the influence of outlying data values than least squares (LS) regression (Wilson 1978; Narula and Wellington 1982), and LAD regression estimators have smaller variances than LS estimators for data that deviate from normality and homogeneous variance, especially with small sample sizes (Wilson 1978; Dielman and Pfaffenberger 1982). Plots of these data indicated nonnormality and that heterogeneous variances were present. Least squares regression lines and r^2 values are given for comparative purposes.

Statistical inferences about proposed and fit regression models (Ho: βfit = βproposed; Ha: βfit $\neq$ βproposed) were made by using a distribution-free permutation test for matched pairs (PTMP; Mielke and Berry 1982) to compare absolute values of the LAD residuals for alternative models. Euclidean distances were used in the PTMP analyses because they are consistent with the geometry of the LAD regressions (Mielke 1986). The combination of LAD regression and distribution-free tests of the LAD residuals is a more desirable approach than transforming variables to meet LS assumptions because it avoids arbitrarily rescaling data into a geometry that is inconsistent with the original measurement scale.

Results

Volume Test

Least absolute deviation regression lines forced through an intercept of 0 (because there can be no volume if there are no trees) produced the following fit model (Fig. 2):

$$Y = 3.21(X),$$

where Y = volume (following Sturman's methods),
X = food SI, computed as $(\mathrm{SIV1} \times \mathrm{SIV2})^{1/2}$.

According to the HSI model, using Sturman's (1968) data, the proposed model should be of the form Y = 10.2(X). Residuals differed between the fit and proposed models ($P = 0.003$), indicating significant differences between slopes of the fit and the proposed models. Plots of these data (Fig. 2), along with least squares regression analysis (Y = 3.91[X], $r^2 = 0.70$), indicate that a positive relation exists between the model output and measured foliage volume.

The plots show that the HSI model assigns high index values to plots that have relatively low levels of foliage volume. The following changes were made in the model to improve the relation (Fig. 3). First, the SI graph for tree canopy closure was modified to obtain maximum SI's at ≥70% canopy closure. The original model (Fig. 1) proposed a maximum SI for this variable between 50 and 75% canopy closure, with decreasing values above 75%. These data indicate that this assumption was not correct for the habitat type studied. The modified relation seems to more accurately depict the effects of changes in canopy closure on foliage volume.

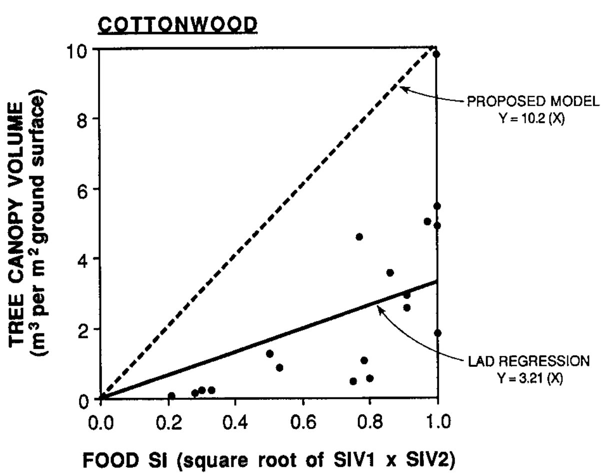


Fig. 2. Plots of original food suitability indices for cottonwood habitats versus tree canopy volume measured following Sturman (1968).

Second, the original variable "average height of overstory trees" considered only the height of overstory trees (defined as trees ≥80% of the height of the tallest tree, where trees are considered to be any woody vegetation ≥5 m in height). Thus, the indirect estimates of canopy volume in stands with a few very tall trees and many trees <80% of the height of the tallest tree would be overrated with the original model because the limited volumes of the many smaller trees would not be averaged with the taller trees. Therefore, the model was revised to consider the average height of all trees. The original model attained maximum SI values at tree heights ≥15 m. These data indicate that volume continues to increase as tree heights increase above 15 m. Therefore, the SI relation was modified to provide increasing values as tree heights increased up to 25 m. In addition, the original model provided SI values for woody vegetation of any height >0 m. Thus, a stand with an average tree height of 5 m would receive an

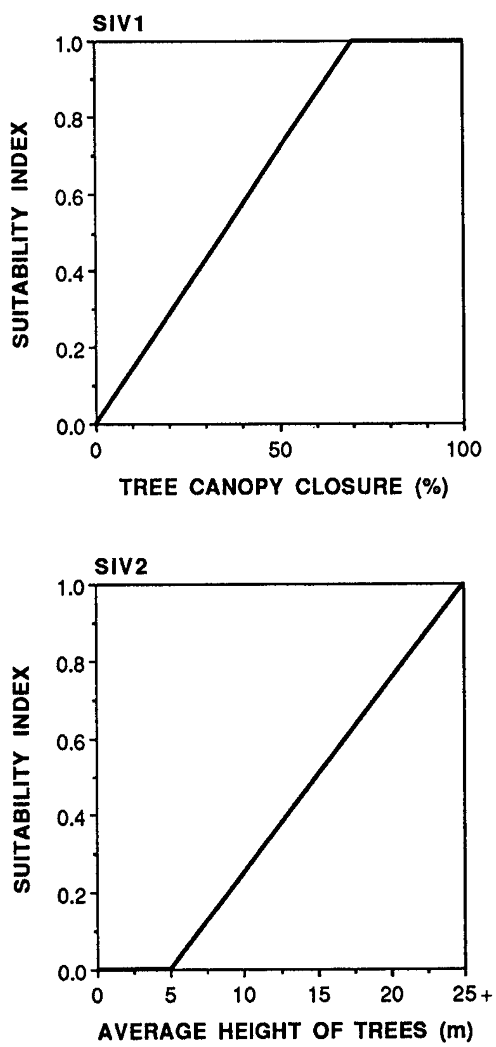


Fig. 3. Revised suitability index graphs for SIV1 and SIV2.

SI of 0.33. These stands would not provide suitable breeding habitat for the black-capped chickadee, which is a forest-dwelling bird. Therefore, the SI relation was modified to provide SI values of 0 for stands with average tree heights of ≤5 m.

The last change made in the model was to eliminate the square root function from the food SI calculation. The volume of a three-dimensional object is equal to the product of the area of the base and the height. For a forest stand, a measure of tree canopy closure is comparable to the area occupied by tree canopies, and a measure of average tree height considers the vertical height. Thus, it is more logical to compute the food SI by using the product of SIV1 (canopy area) and SIV2 (height), rather than the geometric mean.

These model revisions had a marked effect on the ability of the model to predict tree foliage volume. Least absolute deviation regression analysis of the revised food SI relations, forcing a 0 intercept, produced the following fit model (Fig. 4):

$$Y = 10.11(X),$$

where Y = volume (following Sturman's methods),
X = food SI, computed as (Rev. SIV1 × Rev. SIV2).

Residuals from the fit and proposed ($Y = 10.2[X]$) models did not differ ($P = 0.61$), indicating no significant differences between slopes of the fit and proposed models. The least squares regression fit, again with intercept forced to 0, was $Y = 10.39(X)$ ($r^2 = 0.877$).

Data on basal area for each plot were also regressed against volume as computed using Sturman's (1968) methods, and it seems that basal area is a good predictor of foliage volume. Least absolute deviation regression analysis, with the intercept forced to 0, produced the following fit model:

$$Y = 0.138(X),$$

where Y = volume (following Sturman's methods),
X = basal area from plot data (m^2/ha).

Residuals from the fit models and models with a slope of zero were different ($P = 0.05$), indicating the slope of the fit model was significantly different than zero.

HSI Model Test

The test of the volume relation noted previously only considers the model's ability to predict tree canopy volume based on measures of tree height and canopy closure or basal area. A significant additional question is the relation of tree canopy volume to measures of black-capped chickadee abundance. The hypothesis in the HSI model is that habitats will provide increasing potential black-capped chickadee population densities as the HSI increases from 0 to 1.

Both the original and the revised food SI relations were used to test the relation between the HSI and black-capped chickadee population densities from the 10 16-ha riparian cottonwood plots. The model states that the HSI equals the lower of either the food or nest SI values. Population densities, original and revised food SI's, nest SI's, and original and revised HSI values for the 10 plots are provided in Table 2. Least absolute deviation regressions of population densities on the original and revised HSI values produced the following fit models:

Original HSI Model:

$$Y = 0.098 + 0.416(X),$$

where Y = population density of black-capped chickadees (both sexes) per hectare,
X = original HSI.

Revised HSI Model:

$$Y = 0.096 + 2.344(X),$$

where Y = population density of black-capped chickadees (both sexes) per hectare,
X = revised HSI.

Residuals of the fit models and a model with a zero slope did not differ (original HSI model, $P = 0.20$; revised HSI

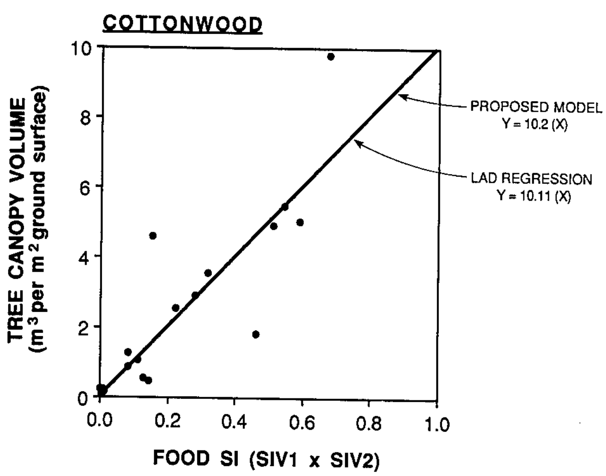


Fig. 4. Plot of revised food suitability indices for cottonwood habitats versus tree canopy volume measured following Sturman (1968).

Table 2. *Black-capped chickadee (*Parus atricapillus*) densities, food and nest SI values, and HSI values for the original and revised models.*

Plot number	Chickadees per hectare	Original food SI	Revised food SI	Nest SI	Original HSI	Revised HSI
1	0.23	0.62	0.097	0.88	0.62	0.097
2	0.39	0.70	0.084	0.81	0.70	0.084
3	0.46	0.62	0.080	0.63	0.62	0.080
4	0.37	0.81	0.102	0.57	0.57	0.102
5	0.30	0.58	0.087	0.39	0.39	0.087
6	0.30	0.68	0.113	0.41	0.41	0.113
7	0.29	0.60	0.071	0.58	0.58	0.071
8	0.10	0.58	0.048	0.19	0.19	0.048
9	0.14	0.47	0.052	0.10	0.10	0.052
10	0.15	0.49	0.021	0.31	0.31	0.021

model, $P = 0.34$), indicating that neither of the fit models differed significantly from a zero slope.

An important aspect of testing HSI models is to compare the model output to an estimate of maximum expected performance of the species. The black-capped chickadee HSI model was developed to encompass the entire range of the species. To determine the highest population densities that have been encountered in previous studies, data from more than 350 Breeding Bird Census (BBC) reports (T. Engstrom, Cornell Laboratory of Ornithology, Ithaca, New York, personal communication) were analyzed. These data indicated that the average density of the highest five BBC's for black-capped chickadees was 1.4 males per hectare (excluding one small orchard with 1 breeding male and a corresponding density of 2.5 males per hectare). Assuming that actual density of both sexes would be double this figure (2.8 chickadees per hectare), a proposed model for an ideal HSI would have the form

$$Y = 2.8(X),$$

where Y = population density of black-capped chickadees (both sexes) per hectare,
X = HSI.

Residuals from the fit model for the original HSI and the proposed ideal model were different ($P = 0.002$), indicating a significant difference between the slopes of these models. This difference can be seen because the fit model for the original HSI yields a predicted population density of 0.52/ha when the HSI is at its maximum value of 1. Residuals from the fit model for the revised HSI and the proposed ideal model did not differ ($P = 0.50$), indicating no significant difference between the slopes of these models. The fit model for the revised HSI predicts a population density of 2.44/ha when the HSI is at 1. Thus, the revised HSI model more closely approximates maximum expected population densities (2.8/ha) when the HSI is at its maximum. The LS regression fit for the revised HSI model was $Y = 0.063 + 2.772(X)$ ($r^2 = 0.425$), yielding a maximum estimated population density of 2.84/ha when the HSI is 1.

Discussion

Volume Test

Proper evaluation of HSI models involves assessing the performance of both the HSI and other testable assumptions within the model. Schamberger and O'Neil (1986) noted that most studies tested the HSI against some measure of population status (Clark and Lewis 1983; Cook and Irwin 1985; Lancia and Adams 1985). Here, I have assessed the performance of both a model assumption and the HSI value.

The foliage volume portion of the tests indicates that the original assumed relation of canopy cover and overstory tree height to foliage volume, although showing a strong linear relation, yielded predictions significantly lower than the volume estimated by Sturman's (1968) methods. Revisions to these model relations resulted in improved predictions of foliage volume.

Habitat Suitability Index model testing can lead to new information if the test is not limited to hypotheses concerning only the variables found in the HSI model. The measurement of tree dbh was added to this study to assess the possibility that basal area could be used to predict tree foliage volume. Basal area data are widely available and are often used in models to predict future forest conditions. Thus, it would be a useful variable for biologists conducting forest habitat studies. Data for the cottonwood habitats indicate that basal area is an excellent predictor of foliage volume. Based on these results, users of the black-capped chickadee HSI model have three reasonable options to estimate foliage volume: Sturman's (1968)

methods, the revised SI graphs and combination formula for tree height and canopy closure, and the predictive model using basal area.

Sturman (1968) provided only two potential tree shapes to be used in calculating foliage volume for an individual tree, one each for conifers and deciduous trees. Many cottonwood trees do not clearly match these shapes. Given the irregular shapes of many trees, I made visual estimates and adjustments of the outer and inner canopy layers to approximate the desired shape. Mawson et al. (1976) described a method to determine tree crown volume using 15 tree shapes. Improved estimates of volume may be possible by expanding the number of tree shapes to match more realistically what is encountered in forested habitats.

HSI Model Test

Results of the test of the HSI as a predictor of black-capped chickadee population density are not as easily interpreted as the volume test results. The fit model for the revised HSI did not differ from the ideal model, whereas the fit model for the original HSI differed significantly from the ideal model. However, both the fit model for the original HSI and the fit model for the revised HSI did not differ significantly from a model with a zero slope. Given the changes made in the revised HSI model and the specific data set used to test the model, several possible explanations can be offered for these results: (1) Whereas the revised model seems to be a better predictor of tree canopy volume, volume may be an inadequate predictor of population densities in cottonwood sites. Additional factors may need to be added to the model to improve its predictive ability; (2) the number of sites ($n = 10$) was inadequate to effectively test the HSI model. If the same spread as in these data occurred over 30 sites, the revised fit model would differ significantly from a zero slope ($P = 0.047$), and thus fail to reject both portions of the null hypothesis. In this same situation (if $n = 30$) the original fit model would continue to be significantly different from the proposed ideal model ($P < 0.0001$), thus rejecting this portion of the null hypothesis; and (3) the 10 sites used for the black-capped chickadee test had too narrow a range of tree canopy cover values (11 to 33%) and average height of trees (7.5 to 12.3 m) to provide an adequate test of the hypothesis. Without further study, it is not possible to determine which of these possibilities best explains the results obtained in this test.

Only a single measure of black-capped chickadee performance (number per hectare) was used in this test. However, population density may be a misleading indicator of habitat quality, as noted by Van Horne (1983). Additional measures of performance, such as nest success or number of young fledged, might improve the test. In addition, the HSI, as a measure of key habitat variables, considers only a subset of all of the factors that may influence individuals and resultant populations. Thus, habitat measurements may indicate ideal conditions, but nonhabitat-related factors (such as disease or severe weather) may cause population declines. The HSI is best viewed as an index of habitat-imposed limitations on a population. For example, an HSI of 1 would indicate no habitat-related limitations exist, whereas decreasing HSI values would indicate increasingly significant habitat limitations. Actual population densities should not exceed the levels indicated by the HSI values but may range below the HSI predictions and not falsify this hypothesis. Specific tests related to this aspect of the HSI have been suggested (U.S. Fish and Wildlife Service 1987, 1989), but the sample size in this study was too small to conduct the tests.

One suggested change in the nest portion of the black-capped chickadee HSI model resulted from this study. The original model required a measure of the number of snags from 10 to 25 cm dbh as an indication of nest site availability. Sedgwick and Knopf (1986), however, noted that snag densities alone do not accurately reflect the availability of suitable nesting substrates in riparian cottonwood stands. The majority of potential nest sites in these stands occurred in cavities in live trees. In eastern hardwood–coniferous forests, use of live trees is much less common (of 44 nests, 41 were in snags or stubs and only 3 were in live trees; Runde and Capen 1987). The best overall measure of black-capped chickadee nest site availability may be the combined density of the number of trees with ≥1 cavity (minimum diameter of 10 cm) and the number of snags (minimum dbh of 10 cm). Further studies are required to test whether regional differences in use of live trees, as opposed to snags, should be incorporated into the HSI model.

I have not developed alternatives to the revised black-capped chickadee HSI model, nor have I attempted to search out the best model (i.e., best statistical fit) from the data. Fitting a new model to these 10 data points may result in a product with no better predictive ability than the current revision. I recommend that additional tests be performed on the revised HSI model before further changes are incorporated. In the interim, I recommend that the revised HSI model be used by field biologists and wildlife managers. The revised model uses the SI relations for canopy closure and tree height illustrated in Fig. 3, the food SI computed as the product of SIV1 and SIV2, and the variable for nest suitability (SIV4) measured as the combined density of the number of trees with ≥1 cavity (minimum diameter of 10 cm) and the number of snags (minimum dbh of 10 cm). Although additional testing is necessary, it seems that the revised model will provide more realistic estimates of both tree canopy volume and black-capped chickadee habitat suitability than the original version.

Acknowledgments

I thank the following individuals for their assistance in the field: J. G. Corn, J. Prasuhn, G. Rowat, and P. J. Sousa. F. L. Knopf and J. A. Sedgwick provided unpublished habitat and chickadee density data for this analysis. B. S. Cade provided statistical assistance. L. A. Brennan, B. S. Cade, R. N. Conner, R. J. Cooper, A. H. Farmer, W. Howe, D. E. Runde, J. A. Sedgwick, W. Slauson, and one anonymous reviewer provided comments on an earlier draft of the manuscript.

References

Barrodale, I., and F. D. K. Roberts. 1974. Algorithm 478: solution of an overdetermined system of equations in the L_1 norm. Commun. Assoc. Comp. Math. 17:319–320.

Bayer, M., and W. F. Porter. 1988. Evaluation of a guild approach to habitat assessment for forest-dwelling birds. Environ. Manage. 12(6):797–801.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72. 202 pp.

Clark, J. D., and J. C. Lewis. 1983. A validity test of a habitat suitability index model for clapper rail. Proc. Southeast. Assoc. Fish Wildl. Agencies 37:95–102.

Cook, J. G., and L. L. Irwin. 1985. Validation and modification of a habitat suitability model for pronghorns. Wildl. Soc. Bull. 13:440–447.

Dielman, T., and R. Pfaffenberger. 1982. LAV (least absolute value) estimation in linear regression: a review. TIMS Stud. Manage. Sci. 19:31–52.

Lancia, R. A., and D. A. Adams. 1985. A test of habitat suitability index models for five bird species. Proc. Southeast. Assoc. Fish Wildl. Agencies 39:412–419.

Lemmon, P. E. 1956. A spherical densitometer for estimating forest overstory density. For. Sci. 2:314–320.

Mawson, J. C., J. W. Thomas, and R. N. DeGraaf. 1976. Program HTVOL, the determination of tree crown volume by layers. U.S. For. Serv. Res. Pap. NE-354. 9 pp.

Mielke, P. W., Jr. 1986. Non-metric statistical analyses: some metric alternatives. J. Statist. Planning Inference 13:377–387.

Mielke, P. W., Jr., and K. J. Berry. 1982. An extended class of permutation techniques for matched pairs. Commun. Statist. Theor. Meth. 11:1197–1207.

Narula, S. C., and J. F. Wellington. 1982. The minimum sum of absolute errors regression: state-of-the-art survey. Int. Statist. Rev. 50:317–326.

Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

Runde, D. E., and D. E. Capen. 1987. Characteristics of northern hardwood trees used by cavity-nesting birds. J. Wildl. Manage. 51:217–223.

Schamberger, M. L., and J. L. O'Neil. 1986. Concepts and constraints of habitat-model testing. Pages 5–10 *in* J. Verner, M. L. Morrison, and C. J. Ralph, eds. Wildlife 2000. University of Wisconsin Press, Madison.

Schamberger, M. L., A. H. Farmer, and J. W. Terrell. 1982. Habitat suitability index models: introduction. U.S. Fish Wildl. Serv., FWS/OBS-82/10. 2 pp.

Schroeder, R. L. 1983. Habitat suitability index models: black-capped chickadee. U.S. Fish Wildl. Serv., FWS/OBS-82/10.37. 12 pp.

Sedgwick, J. A., and F. L. Knopf. 1986. Cavity-nesting birds and the cavity-tree resource in plains cottonwood bottomlands. J. Wildl. Manage. 50:247–252.

Sturman, W. A. 1968. Description and analysis of breeding habitats of the chickadees, *Parus atricapillus* and *P. rufescens*. Ecology 49:418–431.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893–901.

Wilson, H. G. 1978. Least squares versus minimum absolute deviations estimation in linear models. Decision Sci. 9:322–335.

Schroeder, Richard L. 1990. **Tests of a Habitat Suitability Model for Black-capped Chickadees.** U.S. Fish Wildl. Serv., *Biol. Rep.* 90(10). 8 pp.

The black-capped chickadee (*Parus atricapillus*) HSI model was revised based on field studies in Colorado that tested model assumptions regarding prediction of foliage volume. In addition, the relation between bird densities and the revised and original model were analyzed using least absolute deviations regression. Use of the revised model is recommended.

Key words: Black-capped chickadee, *Parus atricapillus*, habitat models, foliage volume, vegetation measurement methods.

Schroeder, Richard L. 1990. **Tests of a Habitat Suitability Model for Black-capped Chickadees.** U.S. Fish Wildl. Serv., *Biol. Rep.* 90(10). 8 pp.

The black-capped chickadee (*Parus atricapillus*) HSI model was revised based on field studies in Colorado that tested model assumptions regarding prediction of foliage volume. In addition, the relation between bird densities and the revised and original model were analyzed using least absolute deviations regression. Use of the revised model is recommended.

Key words: Black-capped chickadee, *Parus atricapillus*, habitat models, foliage volume, vegetation measurement methods.

Schroeder, Richard L. 1990. **Tests of a Habitat Suitability Model for Black-capped Chickadees.** U.S. Fish Wildl. Serv., *Biol. Rep.* 90(10). 8 pp.

The black-capped chickadee (*Parus atricapillus*) HSI model was revised based on field studies in Colorado that tested model assumptions regarding prediction of foliage volume. In addition, the relation between bird densities and the revised and original model were analyzed using least absolute deviations regression. Use of the revised model is recommended.

Key words: Black-capped chickadee, *Parus atricapillus*, habitat models, foliage volume, vegetation measurement methods.

Schroeder, Richard L. 1990. **Tests of a Habitat Suitability Model for Black-capped Chickadees.** U.S. Fish Wildl. Serv., *Biol. Rep.* 90(10). 8 pp.

The black-capped chickadee (*Parus atricapillus*) HSI model was revised based on field studies in Colorado that tested model assumptions regarding prediction of foliage volume. In addition, the relation between bird densities and the revised and original model were analyzed using least absolute deviations regression. Use of the revised model is recommended.

Key words: Black-capped chickadee, *Parus atricapillus*, habitat models, foliage volume, vegetation measurement methods.

U.S. GOVERNMENT PRINTING OFFICE: 1990-773-216/20018